

THE EVOLUTION OF THE RADIO-MEDIAL AREA IN THE WINGS OF THE
MUSCOIDEA ACALYPTRATA (DIPTERA).

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(Thirty Text-figures.)

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Synopsis.

The writer attempts to homologize the venation of the Muscoidea Acalyptrata with that of the Nematocera and Orthorrhapha. As a basis for discussion of the changes involved, the wings of two generalized Nematocera are considered in some detail. The medial field is then traced through the higher Nematocera and Orthorrhapha to demonstrate that, in its essentials, this field has remained unaltered since its first appearance in the Dolichopodidae, and evidence in support of this view is presented. An essay is made to place the *vena spuria* and the vein in the wings of the Syrphoidea and Muscoidea, usually referred to as M_1 , in their correct relation to other parts of the venation, and to show that the *vena spuria* has exercised a profound influence, even in the wings of the most advanced Diptera. Finally, in a series of hypothetical figures, are set out the possible changes that have been necessary to evolve, from the wing of an asilid-bombyliid-like ancestor, the wing of the Muscoidea Acalyptrata.

INTRODUCTION.

During the past hundred years the venation of the dipterous wing has claimed the attention of many students. The need for a venational system early made itself felt in that period of entomology when descriptive work was practically its sole function. Through the efforts of Bates, Wallace, and others, great collections were being built up, and the rapid naming of hosts of newly discovered insects was of prime importance. In answer to this demand, the first venational systems were developed. Two of these appeared in 1862, Loew's system and Schiner's. Both had one feature in common: each was artificial, having as its object the supplying of a rapid and convenient method of notation for descriptive purposes.

The first attempt at a study of wing venation, as contrasted with the mere giving of names or numbers to the veins, was made in 1886, when Josef Redtenbacher propounded his system of venational nomenclature. He realized that the six venational fields were a common inheritance in the wings of all insects. To the principal vein in each of these fields he gave the names accepted today, namely, Costa, Sub-costa, Radius, Media, Cubitus, and the Anal group, and further, he adopted Adolph's conception of the alternation of convex and concave veins, a suggestion which then fell into abeyance until its importance was again recognized by Lameere in 1922.

Using Redtenbacher's ideas as a foundation, Comstock and Needham began their work in 1898, but it was not till 1918 that Comstock, in his book "The Wings of Insects", gave a complete account of the now well-known Comstock-Needham system. Based on morphology and homology, this system, modified as new evidence has become available, has been universally accepted as the only scientific one. Some of the more important modifications have resulted from the work of Tillyard, Alexander and, more recently, Vignon. Tillyard's researches have greatly clarified our ideas of the cubital and anal fields; our present conception of the radial field is the result of Alexander's work. Vignon has made a new study of the dipterous wing as a whole, and while all his conclusions are not yet accepted, there is much in his work that has real value. In Australia, considerable research on the dipterous wing has been done by several workers, but the outstanding contributions to our knowledge of the brachycerous venation have come from Hardy.

If evolution is to have any meaning for us we must regard the higher Diptera as having developed from a more generalized ancestor having many features in common with those of living Nematocera and Orthorrhapha, and it is to these that we must look for aid in the interpretation of the venation of the wing in higher forms. This paper makes no pretence to being a general study of the dipterous wing. I suggest some modification of our concepts of the venation of the medial field and of the area where that field and the radial are contiguous. The examples chosen for discussion are those which appear to me to be our best guides to the interpretation of the venation of this area of the wing in the Muscoidea Acalyptrata.

Evolutionary Trends in the Dipterous Wing.

The general trends of evolution have been to change the contour of the wing and to dispose the venation more effectively. From a long, narrow, petiolate wing, characteristic of the Tipulidae (see Text-figure 1), a shorter, broader one has been developed (see Text-figures 12, 14 and 15). Changes in venation have accompanied those in shape. Whereas, in the primitive wing, numerous veins were disposed over the whole wing area, in the higher Diptera their number is much reduced and they tend to be arranged nearer the costal margin, where their strengthening has given to the wing the reinforcement needed for sustained and rapid movement. To understand clearly these changes and the stages through which they have passed, it will be necessary to discuss the wing venation of some generalized types and then to follow the reduction through forms of increasing complexity until the higher Diptera are met. By this means it will be possible to homologize the veins of specialized forms with those of more generalized types, so giving an insight as to what the veins, present in the wings of the Muscoidea Acalyptrata, really are.

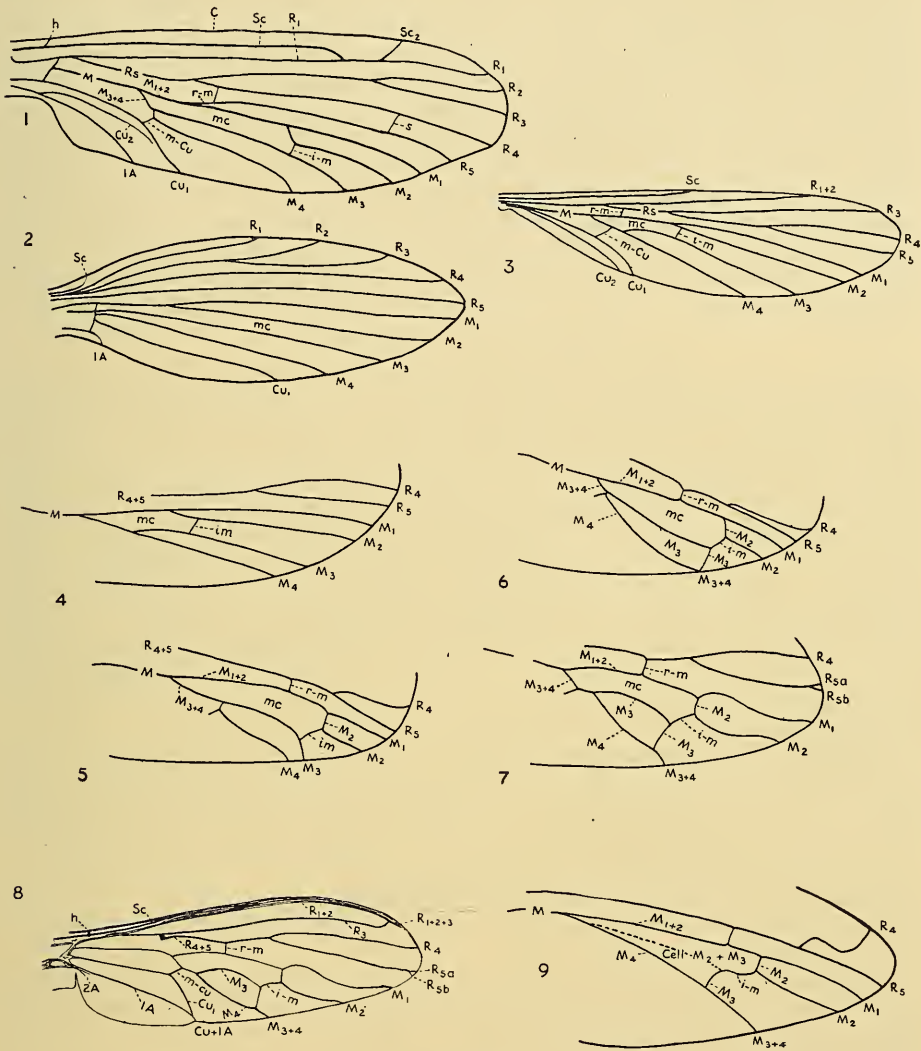
Venation of Two Primitive Living Nematocera.

The most generalized types of venation, in living Diptera, are to be found in the two nematoceros families, the Tanyderidae and the Psychodidae. As representative of these, the wing of *Nothoderus* (Tanyderidae) and that of an undetermined psychodid will serve to illustrate the archaic features of these wings. From the point of view of venation, the Tanyderidae are the most primitive known living Diptera. The wing of *Nothoderus* (Text-figure 1) is long and narrow, the veins being disposed evenly over its whole area. Although considerable reduction has already occurred, it still shows a very full venation. The subcosta still retains its primitive two-branched form, though Sc_2 is already in process of reduction. A complete radial field is present, R_1 and the four branches of R_s all reaching the wing margin as independent veins. The medial field, with its four independent branches, is complete, and the median cell, between M_2 and M_3 , is small, elongate, sub-rectangular in outline, and closed by i-m. It is in the cubital and anal fields that most departure from the wing of the archetype has occurred, since considerable reduction in these fields is obvious. Cu_{1a} and Cu_{1b} have already coalesced to form the single vein Cu_1 , while Cu_2 no longer reaches the anal margin. The first anal vein alone is present, the second and third having been completely suppressed.

The wing of *Psychoda* (Text-figure 2) shows features which indicate an advance on that of *Nothoderus*. The venation is still of a generalized nature and is evenly disposed over the whole wing area, but the length of the wing, relative to its width, is much less. The subcosta is now represented by a single vein only, there being no trace of Sc_2 . The radial field is complete, as is the medial. The median cell is open, the crossvein i-m having been lost. The cubital field has been further reduced by the complete loss of Cu_2 , while a single anal vein, IA (and that short and weak) has been retained.

In both these wings the characters to which I wish to draw attention are the complete five-branched radial field, the complete four-branched medial field, and the small median cell between M_2 and M_3 , in *Nothoderus*, closed by the cross vein i-m. This is the primitive pattern of this part of the wing, a pattern shown in the wings of a very

small number of the older Nematocera only, and one which never reappears later. It is the reduction which these fields undergo in the course of evolution that is the object of this study.



Text-figures 1-9.

1, 2.—Generalized venation in the older Nematocera. 1, Wing of *Nothoderus australiensis* Alexander (Tanyderidae); 2, Wing of *Psychoda* sp. (Psychodidae).

3.—Generalized venation in the older Asilidae; the wing of *Leptogaster* sp.

4-7.—Development of the medial field in the Asilidae. 4, Medial field of *Leptogaster* sp. The small median cell closed by i-m, and the four free branches of the media are primitive characters; 5, Medial field of *Saropogon luteus*. The anal turning of the termination of M_3 is the first stage in the specialization of the medial field; 6, Medial field of *Senobasis mendax*. Basal movement of the termination of M_3 has closed cell M_3 . Veins M_3 and M_4 have united at the wing margin to form one vein, M_{3+4} . Two closed cells in medial field; 7, Medial field of *Laphria* sp. Basal movement along M_4 of point of union of M_3 and M_4 results in vein M_{3+4} becoming of considerable length.

8.—Wing of *Laphria* sp. (Asilidae).

9.—Medial field of *Sphenoidoptera varipennis* (Bombyliidae). The loss of the basal free part of M_3 causes the first appearance of the cell M_2+M_3 . The dotted line in the cell represents the part of M_3 which has been suppressed.

Venation of the Higher Nematocera.

Throughout the sub-order the above general disposition of the medial field is retained, but great changes in the radial field, foreshadowing those by which this field has been produced in the higher Diptera, have occurred in its more advanced members. Alexander (1927 and 1928) demonstrated, in the Tipulidae, the manner in which evolution has brought about the coalescence of R_1 and R_2 to form a single vein reaching the wing margin as R_{1+2} . He further showed that the changes applied not only to the Tipulidae, but equally to all higher members of the order. R_{1+2} is, therefore, a constant in the wings of all Diptera except those few primitive species which still retain both veins as separate entities. Where the union has occurred, R_3 , left as a separate prong of the original R_{2+3} fork, reaches the wing margin as an independent vein, and it, too, occurs in all dipterous wings. In some of the higher Nematocera the R_{1+5} fork, by moving distad, has produced a single compound vein R_{1+5} , but in many, R_1 and R_5 retain their separate identities so that a radial field of four veins, a disposition common in the Orthorrhapha, is formed. The veins are R_{1+2} , R_3 , R_4 and R_5 (see Text-figures 3 and 8).

Venation of the Orthorrhapha.

Just as the more generalized examples of venation are to be found in the lower Nematocera, so it is in the lower Orthorrhapha that is found what may be regarded as the generalized venation of this division. From here onwards there is a strong tendency towards the retention of a four-branched radial field, and it is the medial field that becomes the focal point of reduction. The lower members of the Asilidae form a good point of departure for a consideration of those changes which ultimately lead to the type of medial field characteristic of the higher Diptera. The wing of *Leptogaster* (Text-figure 3) illustrates those features of the venation common to many of the lower Orthorrhapha: the subcosta is a single vein. The radial field is four-branched, R_{1+2} , R_3 , R_4 and R_5 all reaching the wing margin independently. Two cubital branches, Cu_1 and Cu_2 , are present and reach the wing margin. There are no anal veins. The medial field (Text-figure 4) is of the primitive type, consisting of four independent veins, M_1 , M_2 , M_3 and M_4 , all of which reach the wing margin. There is a small, elongate, median cell, closed by i-m.

Specialization of the medial field begins in the Asilidae. An early stage of this is shown in the medial field of *Saropogon* (Text-figure 5), where M_3 , instead of proceeding directly to the wing margin, has its termination diverted towards the anal margin. This tendency in M_3 becomes more pronounced in higher members of the family.

In *Senobasis* (Text-figure 6) further basad movement of the termination of M_3 brings its tip into contact with that of M_4 at the wing margin, thereby closing cell M_3 . The medial field now includes two closed cells—mc and cell M_3 . The combination of veins at the wing margin is M_{3+4} .

The highest of the Asilidae advance a stage further. The point of union of M_3 and M_4 begins to move basad along M_3 , finally attaining the position shown in the medial field of the wing of *Laphria* (Text-figure 7). There is thus brought about a coalescence of the two veins for a considerable part of their length.

Reduction of this field goes no further in the Asilidae, so that consideration of the wing as a whole (Text-figure 8) will illustrate the highest type of venation occurring in the family. The subcosta is a single vein and has considerably shortened. The radial field consists of four branches, R_{1+2} , R_3 , R_4 and R_5 . The union of R_{1+2} with R_3 occurs in the sub-families Laphriinae and Asilinae but, in the Dasyopoginae, R_{1+2} and R_3 both end normally in the wing margin. R_4 and R_5 (the two small branches of R_5 are aberrant) each attains the wing margin and shows a tendency to turn anteriorly towards the wing apex. Of the medial field, three branches reach the wing margin. These are M_1 , M_2 and M_{3+4} . The median cell is small and elongate. Posterior to it lies the closed triangular cell M_3 . The median cell and cell M_3 are closed by three veins or parts of veins. Cell M_3 is closed by part of the vein M_3 while the median cell is closed by i-m and part of M_2 . There are then, lying between M_{1+2} and M_4 , two closed cells. In the cubital field is seen the first stage of the reduction which gives rise later to the small

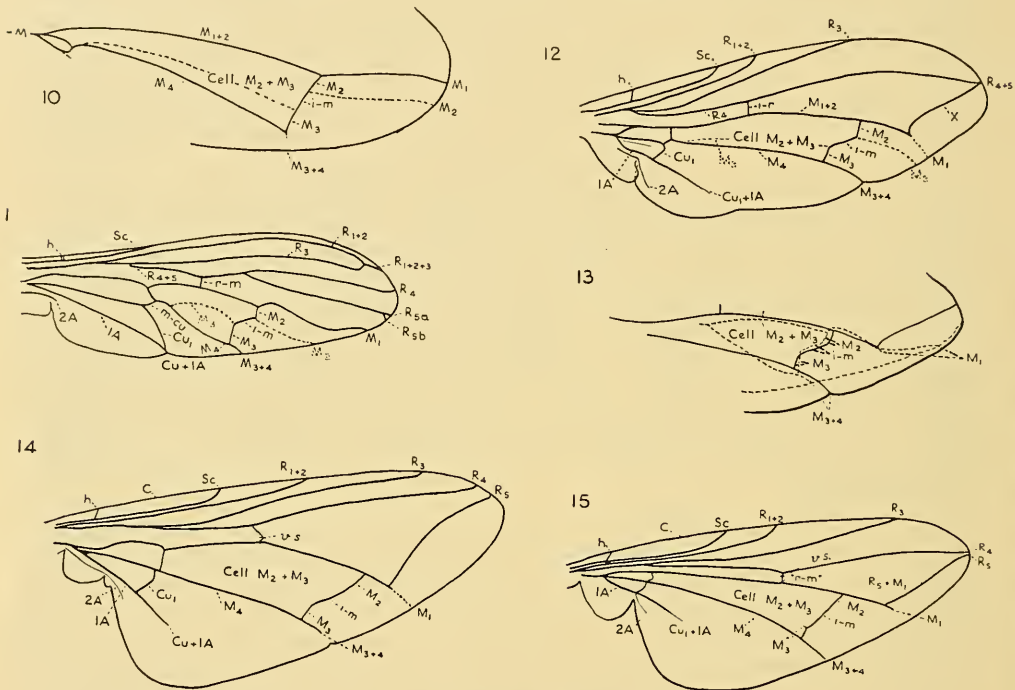
closed cubital cell of the higher Diptera; Cu_1 , by turning basad, has united with 1A, thereby closing cell Cu_1 . Cu_2 is vestigial, as also is 2A.

It is in the Bombyliidae that further stages in reduction are to be found. The radial field remains relatively unchanged. It still retains its four branches but there is a tendency for R_4 to turn apically, and, in the higher members of the family, this tendency, in both R_4 and R_5 , is accentuated. In the medial field, however, very significant reduction has occurred. That of *Sphenoidoptera* (Text-figure 9) has lost the free basal part of M_3 , though three medial branches, M_1 , M_2 and M_{3+4} still reach the wing margin. The loss of the free basal part of M_3 results in the formation of a single, large, closed, sub-triangular cell within the medial field. Anteriorly this cell is bounded by M_{1+2} , and posteriorly by M_1 . This large cell is not homologous with the median cell of lower Diptera and should not be so referred to. It is a compound cell, M_2+M_3 . The identity of the median cell is merged in that of the combined cell, and from here onwards ceases to exist as an independent unit of the venation. Similarly, the "cross vein" closing it is not the i-m of the lower Diptera. It is a serial vein composed of three parts: one of these is the free basal part of M_2 , the second is the free terminal part of M_3 , and these are linked in the middle by the true cross vein, i-m. The "cross vein" so formed I propose to call the serial vein to indicate its true nature and to notate as *se*. Hardy (1947) has shown that a similar course of events has produced the compound cell in the wing of *Lepidostola* (Syrphidae). He is undecided as to whether or not M_2 forms part of the "cross vein" since he states that "the apparent cross vein may include the free basal part of M_2 ". All the evidence, however, supports my contention that the "cross vein" does include part of M_2 . A study of large numbers of dipterous wings has convinced me that its inclusion, together with part of M_3 , is certain in the wings of all Diptera which contain the cell M_2+M_3 , that is, in all Diptera above the Bombyliidae. It is largely due to the failure to recognize M_2 in its correct position that has made impossible a satisfactory interpretation of the medial field in the higher Diptera.

The three-branched medial field, enclosing cell M_2+M_3 , is maintained throughout the Orthorrhapha until the Dolichopodidae are reached, where a highly specialized field is developed. In the higher dolichopodids and in all Diptera higher than this family the terminal part of M_2 between the "cross vein" and the wing margin is suppressed and the medial field characteristic of the Cyclorrhapha makes its first appearance. In *Hydrophorus* (Text-figure 10) the medial field is so disposed. Two branches only of the media are evident; the anterior branch which reaches the wing margin is M_1 , the posterior is M_4 . All that now remains of M_2 , as a separate entity, is that part of it which enters into the formation of the vein, *se*. The only remnant of M_3 is that part incorporated in the "cross vein" and the stub united with the end of M_4 as M_{3+4} .

This advanced type of medial field is so important that some consideration of it in detail is essential. If Text-figure 8 be again referred to, it will be obvious that, if the basal part of M_3 and the distal part of M_2 be eliminated, a similar type of medial field is the result. This has been done in Text-figure 11. The M_{1+2} branch still persists, but, of it, M_1 alone reaches the wing margin; M_{3+4} reaches the wing margin, but the free parts of M_2 and M_3 have lost their identities in linking with i-m to form the serial vein. The important fact to note here is that both branches of M_{1+2} are accounted for, M_1 terminating in the wing margin and M_2 in the anterior part of *se*. This is the disposition of these two veins in all the higher Diptera. If such be correct, we should expect to find, in the higher Diptera, "cross veins" of very irregular shape, indicative of their mode of formation. This is exactly what *does* occur. This angular type of "cross vein" is paralleled, time after time, in the wings of many Tachinidae which have retained evidence of its origin more definitely than have other families of the higher Diptera. It was this fact which, some years ago, caused me to begin the research, the results of which are given in this paper. Such a cross vein is shown in the wing of *Prosenina* (Tachinidae, Text-figure 12). The medial field of this wing is merely a repetition of the hypothetical field of Text-figure 11. This is made even more evident

if the two fields are superimposed, as has been done in Text-figure 13. The "cross vein" and cell M_2+M_3 have the same shape because they have been brought about in an identical manner. Throughout the Muscoidea Calyptrata every variation from the highly angular (*Prosenina*, Tachinidae, see Text-figure 12), through the sinuous (*Cylindromyia*, Tachinidae, Text-figure 14), to the almost straight (*Microtropeza*, Tachinidae, Text-figure 15), cross vein exists. Even in the Muscoidea Acalyptrata (for example, in the families Otitidae and Trypetidae) the sinuous *sc* is not uncommon, though in this group it is usually straight. This straightening of the "cross vein" has hitherto tended to conceal its composite nature in those families in which it occurs.



Text-figures 10-15.

10.—Medial field of *Hydrophorus* sp. (Dolichopodidae).

The suppression of the free basal part of M_3 and the free terminal part of M_2 (shown by dotted lines) has given rise to the earliest appearance of the medial field, typical of that of the higher Diptera. The free parts of M_2 and M_3 are incorporated in the "cross vein".

11.—The wing of *Laphria* sp. (as in Text-figure 8) with the free basal part of M_3 and the free terminal part of M_2 (both shown dotted) eliminated to show how the medial field characteristic of the Tachinidae has been developed.

12.—The wing of *Prosenina* sp. (Tachinidae) showing the serial nature of the angular "cross vein" *sc*. It is composed of the free basal part of M_2 , the free terminal part of M_3 , and the true cross vein *i-m*. Dotted lines represent the former courses of the suppressed parts of M_2 and M_3 . X is the vein discussed later. (The cross vein notated as *i-r* should be *r-m*.)

13.—The medial field of *Prosenina* sp. (Tachinidae—solid lines) superimposed on that of *Laphria* sp. (Asilidae—dotted lines) to show how the medial field of the higher Diptera has evolved from one having asilid-like characteristics.

14.—Wing of *Cylindromyia* sp. (Tachinidae) showing sinuous form of vein *sc*. Note stub of M_1 directed towards wing margin.

15.—Wing of *Microtropeza* sp. (Tachinidae) showing straight form of vein *sc* and the stub of the suppressed free basal part of M_3 .

Venation of the Syrphoidea and Muscoidea Calyptrata.

The location of M_1 and M_2 in their true positions is essential to a correct interpretation of the medial field in the higher Diptera. Because this has not hitherto been clearly understood needless confusion has arisen. A good illustration of this is the

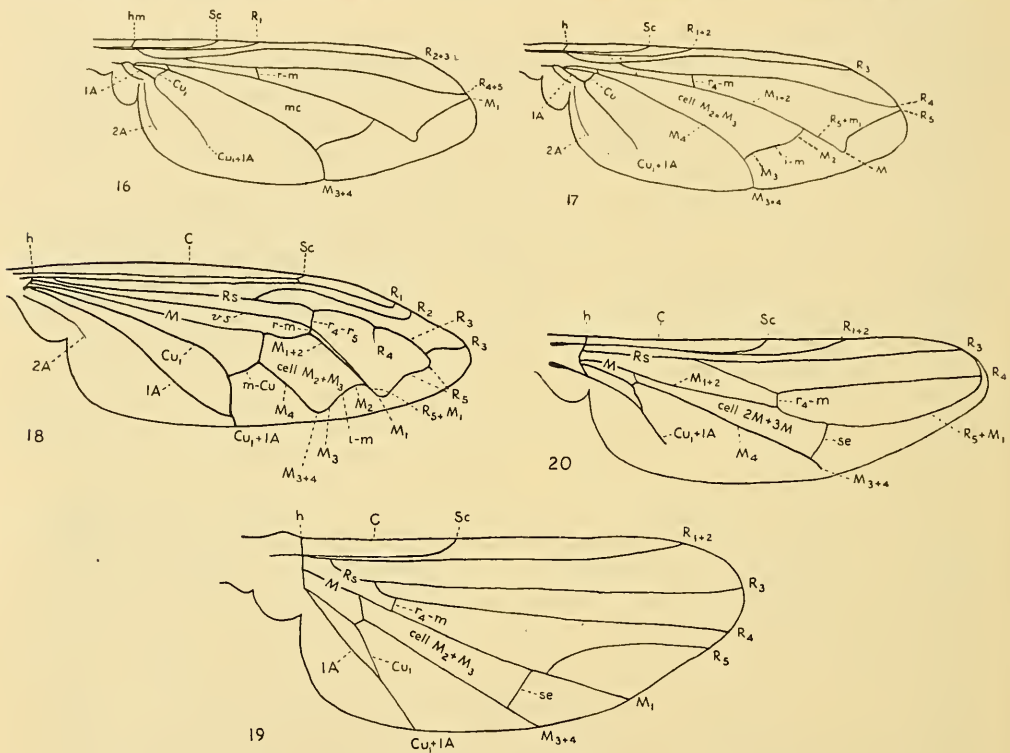
vein which, branching from M_1 , is directed towards the wing apex (see X, Text-figure 12). It is usually notated as M_1 , while M_1 itself is referred to as M_2 ; the actual M_2 in the serial vein is omitted altogether. Whatever this vein may be, it is certainly not M_1 . Text-figures 12, 14 and 15 represent the wings of three species of Tachinidae. In these the termination of M_1 is clearly visible as a stub vein projected towards the wing margin. A fold in the wing membrane connects this stub vein with the margin, and suitable staining defines its former course even more clearly. What has occurred in the muscoid wing is that the termination of M_1 has been suppressed, its remnant being that section of it lying between the serial vein and the end of the stub vein. M_2 , forming as it does part of *sc*, cannot possibly occur in the position in which it is represented.

A further fact which militates against vein X as being M_1 is that of its direction and position. The occurrence of M_1 directed apically is highly exceptional, being found in those families only whose venation is complex. These families are the Mydidae, Apioceridae and Nemestrinidae, and in the wings of each the presence of a four-branched radial field leaves no doubt that the vein posterior to R_5 must be M_1 , or at least a medial branch incorporating it. It would certainly conflict with the principles of evolution of the insect wing if, in all the families of the Nematocera and the Orthorrhapha, M_1 should tend to continue straight to the wing margin or be directed anally, only suddenly to assume a completely new and abnormal position in the Syrphoidea and Muscoidea Calyptrata, and then, equally suddenly, to revert to its normal position in the Muscoidea Acalyptrata and the Hippoboscoidea. Yet this violence to homology has been accepted despite the fact that in both the Syrphoidea and the Muscoidea Calyptrata M_1 is clearly present in its normal position. The truth is that, in the Diptera as a whole, M_1 is remarkably constant in both its position and direction. Text-figures 16 and 17 represent the wing of *Calliphora stygia* Fabr. (Calliphoridae). Text-figure 16 is notated from Tillyard (1926); Text-figure 17 is notated to show the correct positions of M_1 and M_2 .

Vein X, then, not being M_1 as usually understood, there appear to be two possibilities only as to its nature. It is either part of the anterior media, MA, or it is part of the radial field. In the dipterous wing the balance of evidence at present appears to favour the presence of MA, though Tillyard in 1926 (quoted from Hardy, 1947) stated that MA "appears to be entirely missing in most recent orders", thereby contradicting the opinion he had expressed in the previous year. Vignon (1932) claimed MA to be present, stating that the vein usually referred to as R_{4+5} was in reality MA_1 ; in the Syrphidae it is the *vena spuria* which he believes to be MA_1 . Hardy (1947) considers that MA may be present in the Syrphidae, possibly incorporated in the *vena spuria*. The matter is so important, however, that the presence of MA must be demonstrated beyond all reasonable doubt before we can embody it in our scheme of venation, since our so doing will mean an entire recasting of the venation of the dipterous wing, a course which, at this stage of our knowledge, I do not feel to be warranted. Should MA be proven to be present, and Vignon's suggestion that the *vena spuria* is MA_1 be accepted, then I consider vein X to be the vestige of MA_1 , as I believe it to be the functional part of the *vena spuria*. This would align my views with those of Vignon, at least in so far as this part of the wing is concerned. Subject to what has been said above, I shall regard MA as being absent from the dipterous wing and consider the present medial field to have been derived from the original posterior media, MP.

Provisionally rejecting the presence of MA, I believe vein X to be part of the radial field and considerable evidence exists to support this view. The vein makes its appearance in the wings of the Syrphoidea and the Muscoidea Calyptrata only, that is, in those families which have the *vena spuria* either actually present or which retain obvious vestiges of it. These two facts, considered together, suggest that there is some relation between them. Examination of large numbers of syrphid wings shows that the development of the *vena spuria* varies within wide limits among the species and

even among individuals. Sometimes little more than the vestiges where it crosses the so-called r-m can be observed. In other instances it attains a considerable length. In some few examples it is present almost as a complete functional vein. In these latter it appears to have its origin in R_s , and to be directed towards the termination of M_1 , with which it may or may not coalesce. Even when incomplete, the stained wing often shows connections with R_s and M_1 . In *Microdon* (Text-figure 18) it is practically complete, its distal end making contact with M_1 near the termination of the latter. From here it continues towards the wing apex as a functional vein. My interpretation, therefore, is that the *vena spuria* is R_5 and hence vein X is R_5 (Text-figure 18, and see Text-figures 14, 15 and 17). This means that in existing syrphids



Text-figures 16-20.

16, 17.—Wing of *Calliphora stygia* Fabr. (Calliphoridae). 16, Notated from Tillyard (1926); 17, Notated to show correct positions of M_1 and M_2 . Rest of notation as explained in text. (R_5+m_1 should be R_5+M_1 .)

18.—Wing of *Microdon fulgens* (Syrphidae) showing the venational pattern from which developed that of the higher Diptera. Note the very complete *vena spuria* (*v.s.*) and its connections. The terminal part of the *vena spuria* turns apically after coming in contact with M_1 .

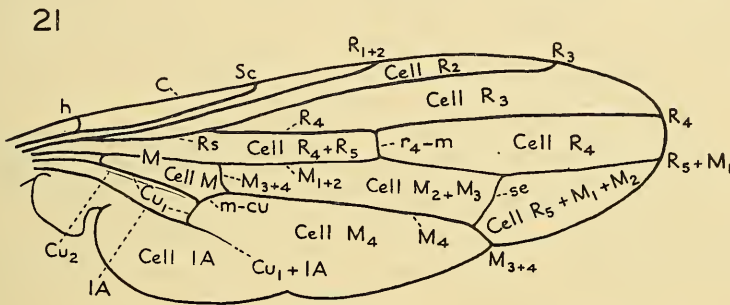
19.—Wing of *Platypezoides diversa* (Platypezidae) showing fusion of R_5 with M_1 .

20.—Wing of *Chrysomya aenea* (Otitidae) showing the apical trend of R_5+M_1 , an example of the influence exerted on the combination by R_5 .

the functional part of the *vena spuria* is R_5 . Hardy (1947) questions the presence of R_5 in the wings of Syrphidae without denying the possibility of its occurrence. I believe that, when the *vena spuria* has been more widely studied, my contention that it is R_5 will be upheld. If the higher Diptera have developed from simpler forms allied to the lower, it seems difficult to deny to the Syrphidae the presence of R_5 , which is a constant in the wings of the Nematocera and the Orthorrhapha. This would mean that the three radial branches in cyclorrhaphous wings are R_{1+2} , R_3 and R_4 , with the vestiges of R_5 still retained as an independent vein in Syrphoidea and the Muscoidea Calyptрата. The cross vein, usually referred to as r-m, therefore connects not R_{4+5} with M_{1+2} , but R_4

with M_{1+2} , passing across R_5 as it does so. The true r-m is the posterior section of this vein.

The Muscoidea Calyptrata retain vestiges only of the *vena spuria*, but its former course across "r-m" is often defined by a noticeable angularity in "r-m" with short stubs of the original vein on either side (see Text-figures 14 and 15). When these are present, folds in the wing membrane connect them with R_s basally and with the tip of M_1 distally. In such cases the only part of R_5 that remains is the vein X (see Text-figure 12). The course of events, from the fully developed *vena spuria* to the final result as above, may have been brought about in the following manner: R_5 originally left R_s as a separate vein directed towards the tip of M_1 , near where it turned sharply in an apical direction as other branches of the radius tend to do. Ultimately, union occurred between R_5 and M_1 , and since M_1 now took over the functions previously performed by that section of R_5 between R_s and M_1 , disintegration of this section began. An early stage of the reduction is represented in the wings of those Syrphidae in which the *vena spuria* is most complete (see Text-figure 18). With the passage of time the whole section was eliminated, its only vestige occurring where the vein crossed



Text-figure 21.

Wing of *Sapromyza ocellaris* Malloch (Lauxaniidae) to show the system of notation used in this paper for the wing of the Muscoidea Acalyprata.

"r-m" (see Text-figures 14 and 15). In a later stage of development M_1 ceased to reach the wing margin (see Text-figure 15) and the distad movement of the point of union of R_5 and M_1 resulted in the coalescence of the two veins as R_5+M_1 (see Text-figure 20). The tendency for fusion to occur between R_5 and M_1 is early shown in the course of evolution. In varying degrees of completeness it is found in the wings of many Orthorrhapha. In the Tabanidae coalescence occurs, in most cases at the distal ends of the two veins, near the wing margin. More advanced examples of fusion occur in the Dolichopodidae, but it can best be seen in the wings of Platypezidae (Text-figure 19, *Platypezoides*) and Pipunculidae.

Venation of the Muscoidea Acalyprata and Hippoboscoidea.

The culmination of the process of reduction is attained in these groups, and the preceding discussion has been a necessary introduction to a satisfactory interpretation of the venation, more particularly of the Muscoidea Acalyprata. Further specialization eliminates even the vestiges of R_5 as a separate vein, its identity being merged in that of M_1 . Nevertheless, the influence of R_5 is still noticeable in certain of the Otitidae, Tanypezidae and Calobatidae, in which a strong tendency is shown for R_5+M_1 still to be directed apically, as in *Chrysomyza* (Otitidae, Text-figure 20). In the higher families, such as the Lauxaniidae, this tendency is lost, R_5+M_1 continuing more or less directly to the wing margin. There is thus produced the venational plan which is characteristic of the most advanced Diptera.

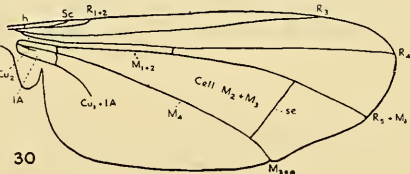
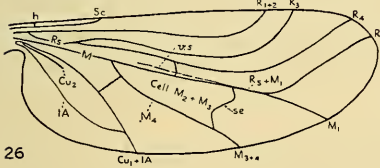
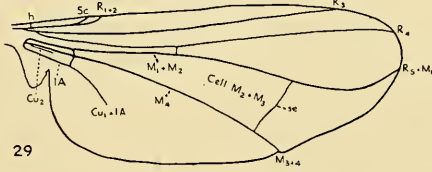
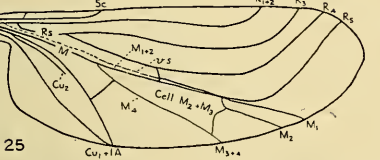
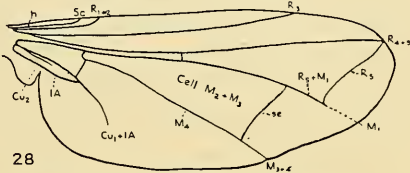
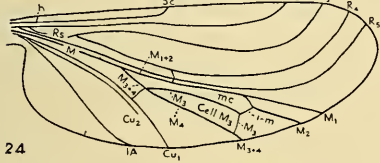
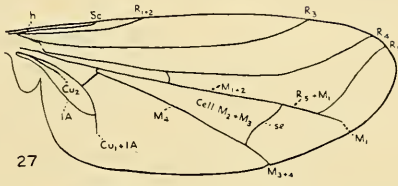
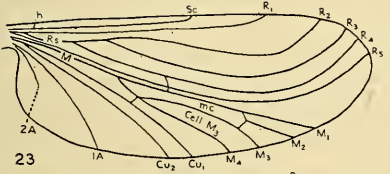
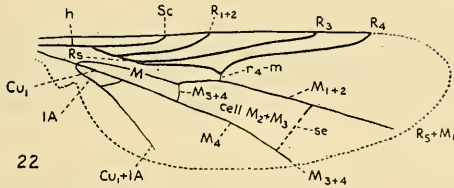
Sapromyza ocellaris Malloch (Lauxaniidae, Text-figure 21) exemplifies this type of venation. The number of veins has been greatly reduced, they tend to be reinforced in the anterior part of the wing, while large open cells occupy much of its posterior

region. A noticeable feature is the small number of closed cells, the result of the loss of cross veins, of which three only, "r-m", i-m incorporated in *se*, and m-cu remain. To indicate the true nature of "r-m" which bridges not R_{1+5} and M_{1+2} , but R_4 and M_{1+2} , I notate it as r_4 -m. The subcosta is always short, making contact with the costa less than half-way along the margin. R_{1+2} is also short, and in many families its tip occupies the position formerly occupied by that of Sc. This results in the elimination of Sc, of which only a vestige remains near the wing base. If present, the sub-costal cell is small, but the basad movement of the termination of R_{1+2} often results in its obliteration. Cell R_2 is attenuated. R_5 gives rise to two branches. The anterior of these is R_3 , a long vein, more or less parallel to R_{1+2} , and terminating in the wing margin. The posterior branch is R_1 , which continues independently to the wing margin. Of R_5 the distal part only remains, fused with M_1 . The medial field consists of two branches. The anterior branch is M_{1+2} as far as the serial vein, where M_2 turns anally to form part of that vein. M_1 united with the vestiges of R_5 reaches the wing margin as R_5+M_1 . The posterior branch of the media is M_1 , which unites with the vestige of M_3 in the serial vein and reaches the wing margin as M_{3+4} . The large cell, bounded anteriorly by M_{1+2} and posteriorly by M_1 , is cell M_2+M_3 . This is closed by the serial vein *se*, composed of i-m, joined to parts of M_2 and M_3 . Cell M_1 is very large. Cu_1 , after forming the posterior boundary of cell M, turns anally and unites with 1A. The vein Cu_1+1A , so produced, is always short, never reaching the wing margin. Vestiges of Cu_2 and 2A sometimes occur near the wing base.

The venation of the Hippoboscoidea (Text-figure 22) is difficult of interpretation in the medial field by reason of further reduction. The serial vein, *se*, appears to have been eliminated, leaving cell M_2+M_3 open, but until I have a large collection of this superfamily available for study my suggestions can only remain tentative. It is often the exceptional individual which provides the key to difficulties, otherwise insuperable, and such are more likely to occur when there is ample material for examination. The effects of reduction have been to strengthen the veins of the radial field at the expense of those of the medial, and in these circumstances the loss of *se* would be a not unexpected result. Whether this has or has not happened will not affect the rest of the venation, which is modelled on that of the Diptera Acalyptrata.

Conclusions and Discussion.

As pointed out earlier, discussion of the venation of the lower Diptera was not an end in itself. I have used it in the elucidation of some difficulties of interpretation in the radial and medial fields of the Muscoidea Acalyptrata, and my conclusions are those stated above. I believe this venational type to have been derived from one having affinities with those of both the Asilidae and Bombyliidae. Such a wing may have been not unlike that of Text-figure 23. Text-figures 24-30 represent possible changes that occurred, culminating in the wing of *Sapromyza* (see Text-figure 21). The wing in Text-figure 23 combines a complete bombyliid-like radial field with a complete asilid-like medial field. In Text-figure 24 reduction has already resulted in the coalescence of R_1 and R_2 and the closure of cell M_3 . Text-figure 25 shows the formation of the combined cell M_2+M_3 by the loss of the free basal part of M_3 , while R_5 is degenerating into the *vena spuria*. In Text-figure 26 the loss of the terminal part of M_2 gives rise to the final development of cell M_2+M_3 , which is closed by *se*. The basal part of R_5 is almost suppressed. In Text-figure 27 *se* is tending to straighten while only the free terminal part of R_5 remains. M_1 is being reduced and no longer reaches the wing margin. Text-figure 28 represents a further stage of Text-figure 27. In Text-figure 29, M_1 has lost its identity by its coalescence with R_5 , the influence of which is still shown by the direction taken by R_5+M_1 . Text-figure 30 is the typical wing of the Muscoidea Acalyptrata. A comparison with Text-figure 23 shows the very great reduction which has occurred. These changes may be summarized as follows. Throughout the series there has been a great reduction in the number of veins and their disposition has been completely changed. Their general costad movement has produced large areas in the posterior part of the wing membrane where venation is absent. The veins towards the



Text-figures 22-30.

22. Wing of *Ornithomyia* sp. (Hippoboscidae) to show the maximum of reduction in the dipterous wing. Note strengthening of anterior veins and corresponding weakening of the veins in the posterior region of the wing. The dotted line shows the position of the suppressed *se*.

23-30.—Possible stages in the evolution of the wing of the Muscoidea Acalyptata. 23, Wing of hypothetical orthorrhaphous ancestor. A five-branched bombyliid-like radial field and a four-branched asilid-like medial field are present. The median cell is small and elongate. 24, R_1 and R_2 have fused to form R_{1+2} . A four-branched radial field, R_{1+2} , R_3 , R_4 and R_5 , is produced. Basal movement of the termination of M_3 has closed cell M_3 and the combined vein M_{3+4} has been developed. This results in the reduction of the medial field to three branches reaching the wing margin M_1 , M_2 and M_{3+4} . 25, Following the coalescence of its distal part with M_1 , the base of R_5 is disintegrating to form the *vena spuria*. Cell M_2+M_3 has been formed by the suppression of the free basal part of M_3 ; the medial field still has three branches reaching the wing margin. 26, Further disintegration of the *vena spuria* occurs; the radial field still remains four-branched. The medial field has completed its development by losing the free terminal part of M_2 . Two branches only of the media now reach the wing margin M_1 and M_{3+4} . The angular "cross vein" *se*, by its shape, still shows its components. 27, R_{1+2} is shortening. M_1 now fails to reach the wing margin. The "cross vein" *se* is straightening. All trace of the *vena spuria* is lost except for the angularity in r_1-m , where it previously crossed. The fusion of R_5 and M_1 is proceeding. 28, R_{1+2} is very short. Most of the free terminal part of M_1 has been lost. Cell Cu_1 almost complete. 29, Influence of R_5 still shown by apical turn in R_5+M_1 . All trace of M_1 as an independent vein lost. Cell Cu_1 complete. 30, The wing of the Muscoidea Acalyptata. For complete notation see Text-figure 21.

costal margin are strengthened; those nearer the anal margin are weakened. I have attempted to explain these changes logically, using as evidence in support of my contentions the information available in the wings of living Diptera. With the exception of the hypothetical development series (Text-figures 23-30), all wings figured are those of actual insects.

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My thanks are due to Miss Helen M. Brookes, who assisted with the lettering of the Text-figures, and to Miss Margaret E. Morphett, who also helped with the lettering and drew Text-figure 8.

Note on Staining Methods.

In clarifying doubtful parts of the venation, such as unions between veins, and the courses previously taken by veins now suppressed, I have found suitable staining invaluable. Various stains, and methods of using them, were tried before the following method was adopted as being the most satisfactory. The stain used consists of one gramme of basic fuchsin dissolved in 100 c.c. of 95% alcohol. Wings, removed from freshly killed insects, were dropped into 95% alcohol, in which they were allowed to stand for half an hour before transferring to the stain. Wings from dried insects were put directly into the stain. Staining occurs very slowly, a desirable feature, since the process is at all times completely under control. The bases of the long veins first take up the dye, which then moves slowly along them until they are completely stained. Very prolonged immersion is necessary before absorption by the wing membrane begins, though areas in which veins have been recently suppressed absorb the dye more easily than those which have not been veined or in which venation has long been lost. Determined by what the operator is aiming at, staining, even for periods of four to six weeks, may not be too long. Every few days the wings are removed, washed in 95% alcohol, and examined under the microscope to note the extent of the staining. When this is sufficient for the purpose in view, they are immersed in absolute alcohol for half an hour, then in xylol for the same length of time, and mounted. Since basic fuchsin is sensitive to even the slightest trace of acid, some neutral mountant must be used. For permanence and best retention of colour "Sira" was found to give the best results.

References.

- ALEXANDER, C. P., 1927.—The Interpretation of the Radial Field of the Wing in the Nematoceros Diptera, with Special Reference to the Tipulidae. *Proc. Linn. Soc. N.S.W.*, 52, 42-72.
- , 1928.—A Comparison of the Systems of Nomenclature that have been Applied to the Radial Field of the Wing in Diptera. *Proc. Fourth Intern. Cong. Entom. Cornell, U.S.A.*, 700-707.
- HARDY, G. H., 1947.—The Wing Venation of Syrphidae. *Entom. Month. Mag.*, 83, 142-144.
- , 1947.—Miscellaneous Notes on Australian Diptera. XIII. The Origin of the *Vena spuria*. *Proc. Linn. Soc. N.S.W.*, 72, 229-232.
- TILLYARD, R. J., 1926.—The Insects of Australia and New Zealand, p. 369.
- VIGNON, P., 1932.—Nomenclature des veines de l'aile chez les Diptères. *Encyc. Ent. Dipt.*, 6, 133-142.